Title: Land-use alters soil propagule banks of wetlands down the soil depth profile

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Abstract:

Many studies have investigated the effects of human disturbances on floodplain propagule banks, but few examine how these propagule banks change down the soil depth profile. Changes in soil propagule banks with depth can indicate the state of past vegetation and potentially demonstrate the effects of different land-uses on the soil profile. Here, we examined changes in soil propagule banks down the soil depth profile in an Australian floodplain wetland with five different land-use histories ranging from a relatively minor disturbance (clearing) through to more major disturbance (continuous cultivation). Land-use had a larger influence than floodplain geomorphology on the propagule distribution of wetland plant group numbers. An observed decrease in individuals over the depth profile also altered terrestrial plant groups in fields with longer land-use histories. Overall, soil propagule profiles for terrestrial plants were not as affected by land-use as those of wetland plants. The geomorphological position on the floodplain also altered the soil propagule bank, with areas subject to the most flooding having the highest number of wetland species and retaining more of these species with greater depths. In conclusion, land-use impacts alter soil propagule banks down the profile, despite most studies focussing on the top few centimetres.

Keywords: restoration, seed, agriculture, flood frequency, floodplain wetland, propagule bank

Introduction:

By directly altering standing vegetation, agricultural land-use, including cultivation and grazing, can indirectly alter the composition and structure of soil propagule banks in floodplain wetlands at the surface or to a few centimetres depth (~ 5 cm), with significant implications for patterns of vegetation regeneration (Wienhold and van der Valk, 1989; Hölzel and Otte, 2001; Middleton, 2003; O'Donnell, Fryirs & Leishman, 2014; Dawson, *et al.*, 2017a). Little research, however, has examined how different disturbances affect plant propagule banks with increasing soil depth. While the abundance and richness of propagules in soil propagule banks typically decline with depth, the rate of decline can depend on various factors including (but not limited to) vegetation type, the length of time over which a wetland has been drained, and the condition of standing wetland vegetation (van der Valk and Davis, 1979; Wienhold and van der Valk, 1989; Godefroid, Phartyal and Koedam, 2006). Soil propagule banks in wetlands are usually deeper than those in terrestrial ecosystems (Nicholson and Keddy, 1983; O'Donnell, Fryirs and Leishman, 2014), with viable propagules germinating from sediment samples taken as deep as 35 cm (van der Valk and Davis, 1979). Deeply buried seeds tend to be older and include species that form persistent propagule banks or propagule banks that are more resistant to disturbance (Godefroid, Phartyal and Koedam, 2006). Further, changes in the soil seed or propagule bank can indicate characteristics of past vegetation or the level of past disturbances (van der Valk and Davis, 1979; Godefroid, Phartyal and Koedam, 2006). Although most germination from floodplain soil propagule banks is likely to occur from propagules in the top of the soil profile, deeper seeds may potentially be moved to the surface via flooding or other disturbances, meaning that the deep propagule bank could act as a propagule source for regenerating wetlands. Furthermore, examining the depth profile of plant propagule banks can demonstrate the extent of soil degradation or what changes may have occurred over time as soil layers accumulate, and may reveal levels of resilience of propagules to anthropogenic disturbances.

Assisted natural restoration is common in degraded wetlands, where degrading processes are halted and "natural" water regimes (either managed or unmanaged) are reinstated, with the assumption that wetland revegetation will occur from the soil propagule bank and colonising species (Wienhold and van der Valk, 1989; Donath, Holzel and Otte, 2003; Middleton, 2003). However, restoration often follows an alternative trajectory where other types of vegetation

(e.g. terrestrial shrubs) rapidly colonise instead of wetland species (Suding, Gross and Houseman, 2004; Moreno-Mateos *et al.*, 2015). In general, degradation of floodplain wetlands in Australia leads to the soil propagule bank in the top 5 cm holding fewer wetland plant species, more exotics and more terrestrial species than non-degraded floodplain wetlands (Robertson and James, 2006; Dawson, *et al.*, 2017a). In a previous study focused on the top 5 cm of soil from the same area (Dawson, *et al.*, 2017a), we showed that soil propagule banks in fields with histories of longer cultivation had compromised restoration capability. However, fields with few years of cultivation, or fields that were only cleared, showed less signs of disturbance. We concluded that with time and flooding, these soil propagule banks had the potential to restore wetland vegetation composition (Dawson, *et al.*, 2017a). While this, and other studies focusing on the top 5 cm of soil, have led to an understanding of the effects of degradation on close-to-surface floodplain wetland propagule banks, we are not aware of any studies based in Australia that have examined past land-use effects on the propagule bank down the sampled soil depth profile.

In this study, we examined changes in the soil propagule bank down the soil depth profile in a wetland on retired agricultural land in the Macquarie Marshes, Australia. We investigated this in five fields with a range of disturbance histories that spanned a single clearing event with a bulldozer 14 years before sampling, through to being cultivated continuously for 23 years and then left to restore for five years before sampling was conducted. We sought to examine how past disturbances changed the propagule bank down the soil depth profile and to determine which wetland plant groups were most affected. Further, we also explored whether the amount of flooding a site received before sampling changed the soil propagule bank down the soil depth profile, using the proxy of geomorphological floodplain position. Specifically, the two questions we address are: 1) Does the soil propagule bank depth profile change with past land-use and which wetland plant groups are most affected? and 2) How does past disturbance (land-use history) and floodplain position affect the soil propagule bank with increasing depth?

We hypothesised that the more intensive past land-uses (i.e. continuous cultivation) would show effects deeper into the soil profile of the propagule bank and that wetland plant groups and native species would be the most affected – as indicated by lower numbers of individuals from the wetland plant groups. This is because we assumed that the effects of repeated years of cultivation would eventually degrade the soil propagule bank deeper than where land use had only comprised clearing or fewer cultivation events. As part of this hypothesis, we

thought that fields that had been cultivated rather than only cleared would show a greater effect, as would those fields that had been disturbed more recently. Further, we anticipated that sites geomorphologically prone to flooding would have higher numbers of wetland plant groups and native species, as flood regimes that are less modified or more similar to historical regimes favour native species (Catford *et al.*, 2014; Dawson, *et al.*, 2017a). Consequently, we expected such sites to show greater abundances of wetland seeds in the upper layers of the soil profile reflecting the restoration of propagule banks after flooding.

Methods:

Study site: This study was conducted in a revegetating floodplain wetland, part of the Macquarie Marshes, south-eastern Australia (Fig. S1; 147.55°E 30.8°S). The Macquarie Marshes consists of a range of a flood-dependent vegetation communities that reflect the local inundation regime. This inundation regime is driven by upstream rainfall events, as local conditions are dry (<500 mm rainfall per annum) and relatively warm (daily temperatures range between 4-16°C in winter and 20-36°C in summer). The most regularly flooded vegetation communities are *Typha domingensis/orientalis* and *Phragmites australis* reed-beds, with *Paspalum distichum* grasslands, which are inundated annually. Slightly higher elevations that are still frequently inundated support river red gum (*Eucalyptus camaldulensis*) forests and lignum (*Duma florulenta*) swamps, both with understories of amphibious wetland (mainly native) species. The highest elevations support black box (*Eucalyptus largiflorens*) open woodland with terrestrial understorey species (e.g. grasses and chenopods; (Bowen and Simpson, 2010; Thomas *et al.*, 2010). While the vegetation varies along an elevation-gradient, the entire area is very flat, with an average rise of less than 1 m every 2.4 km in the study area (Hesse 2009; Yonge & Hesse 2009).

The Macquarie Marshes is part of the Murray-Darling Basin, where river regulation and water diversion for irrigation have led to degraded floodplain vegetation communities (Catford *et al.*, 2011, 2014) with the Marshes no exception (Kingsford and Thomas, 1995; Bino *et al.*, 2015). In the late 2000s, several initiatives were undertaken to restore these degraded vegetation communities, including the purchase of 2,436 hectares of land (Pillicawarrina property), along with its 8,658 ML water licence (Department of Environment Climate Change and Water NSW, 2011). Historically, vegetation on this property would have been similar to the rest of the Marshes until it was progressively cleared for grazing and

cultivation (Paijmans, 1981; Kidson *et al.*, 2000; Dawson *et al.*, 2016). Different fields had different land-use histories, ranging from continuously cultivated from 1985 until 2008, to cleared once in the late 1980s (L. Johnson, pers. comm., 2014 Pillicawarrina property manager; Waters 2011; Dawson, Kingsford, Berney, Keith, *et al*. 2017). In addition to clearing and cultivation, artificial levee banks ('dikes') were constructed adjacent to the river which held back all but the highest flows, significantly decreasing river/floodplain connectivity (L. Johnson, pers. comm., 2014 Pillicawarrina property manager; Dawson, Kingsford, Berney, Keith, *et al*. 2017).

In 2009, when the property was purchased by the government, cultivation ceased and management focussed on revegetation, with the aim of restoring vegetation communities to a similar character as those of undisturbed sites (Waters, 2011; Berney, 2012). Aside from the cessation of agricultural land-use, the only other active management intervention was to breach the levees at strategic points and enlarge culverts in June 2010 to enhance water passage between the river and floodplain (Hesse, 2009; Department of Environment Climate Change and Water NSW, 2011; Dawson, *et al.*, 2017a). The timing of this was fortuitous as a decade-long drought in the Macquarie Marshes was broken by natural floods, supplemented with environmental flows in the 2009/2010, 2010/2011 and 2011/12 flooding seasons.

Soil sampling: In January 2014, we sampled the propagule bank at 45 sites within five fields of differing land-use histories and three floodplain positions (a subsample of sites from Dawson *et al*. (2017; Fig. S1). The fields' land-use histories were:

i. cleared with bulldozer in 2000 ("Clear. 2000");
ii. cleared with bulldozer and ripped with bulldozer tines in 2003 ("Clear. 2003");
iii. cultivated in 2003 ("Cult. 2003");
iv. cultivated in 2006 ("Cult. 2006"); and
v. cultivated from 1985-2008 ("Cult. 85-08").

Each field had nine sampling sites that were evenly stratified across three geomorpholgical floodplain positions:

a. floodplain micro-channels (Channel);
b. immediately adjacent to these micro-channels (Riparian); and
c. 50-100 m from the micro-channels (Plain; Dawson, Kingsford, Berney, Keith, *et al*. 2017).

These floodplain micro-channels (<20 cm deep; Hesse 2009) were identified using a LIDAR-based digital elevation model (DEM; Steinfeld *et al*. 2013).

At each site, we collected soil samples at 5 cm increments down to a maximum depth of 30 cm with a sampling pipe that had a diameter of 5 cm (area = 19.63 cm^2, volume = 98.15 cm^3). Throughout the rest of the manuscript, numbers are presented for this volume only and we have not scaled the data, unless specifically stated otherwise. Two of the sites (Plain sites in Cult. 2003 and Cult. 2006), however, had such hard and dry clay that it was only possible to take samples down to a depth of 25 cm. Samples were then air-dried and stored in the dark for 5 months. Although we also conducted vegetation surveys at the same time, extremely dry conditions meant that very few annual species were present, so the observations were not representative of the plant communities that typically occur after inundation and therefore not used in analyses.

Germination methods: We germinated propagules in the greenhouse over two months (June-July 2014). The greenhouse was heated to 20-27 °C, similar to spring temperatures in the Macquarie Marshes. Soil samples were spread as thinly as possible in plastic containers filled with steam-sterilised potting soil to a depth of 3 cm. Experimental containers were then laid out randomly on benches and re-randomised every two weeks. Watering occurred twice daily and samples were allowed to drain freely as a previous study found this watering regime produced the greatest number of germinants (Dawson, *et al.*, 2017a). Germinants of angiosperms and pteridophytes were counted, identified and removed every two to three days to avoid competition (Capon, 2007). We refer to all emerging plants as 'germinants' for communication ease, although we recognise that some plants may have originated from spores and vegetative propagules rather than seeds. Unidentified germinants were re-potted separately and grown until diagnostic features developed. Where many germinants emerged simultaneously (e.g. rush species or some grass species), only a subset were grown until identification was possible. Species were then categorised into nine wetland plant groups defined by first taking Brock and Casanova's (1997) six functional groups (no submerged species germinated) and then subdividing into native status according to the Australian National Botanic Gardens (Table 1; following Dawson *et al*. 2017; http://www.anbg.gov.au/apni/index.html). The rush species complex was analysed separately from the other amphibious tolerant emergent species as they dominated germination numbers

and we wanted to distinguish what was happening in this species complex from the rest of the plant group.

Data analyses: Data were analysed using the Hierarchical Modelling of Species Communities (HMSC) package in R (Ovaskainen *et al*. 2017, Tikhonov *et al*. (in prep)). This package uses joint species distribution modelling framework (Warton *et al.*, 2015), with a Bayesian evaluation to examine community data with species' abundances (Ovaskainen *et al.*, 2017). The 'species' in our data were the 9 plant groups and 45 sites (9 sites in five fields), out of which seeds germinated in 237 samples out of a possible 268 samples (6 depth samples per site, minus the two missing deeper plain sites). Three values were omitted from the analysis as they were outliers in each of the plant groups (more than double the next largest value) and affected the ability of the model to converge: 93 amphibious tolerator low-growing germinants in the Clear. 2003 field, 34 terrestrial damp exotic germinants in the Cropped–85-08 field, and 241 terrestrial damp native germinants in the Clear. 2003 field. Samples where seeds did not germinate were still included in the model - but had 0 abundance for all plant groups.

Our model included three explanatory variables: land-use history, floodplain position and sample depth. Sample depth was entered as a continuous variable and the interaction between sample depth and both land-use history and floodplain position was included in the model terms. The intercept used in the model was the field with the least disturbance, Clear. 2000 and plain sites for the geomorphological position. There were also two random variables in the model, one to account for the nested sampling design of floodplain position within each field and another at the site level, to account for depth samples coming from the same site. A lognormal (overdispersed) Poisson distribution was used in the models as the transformed variance was close to the mean (1.8 and 1.4 respectively), but still skewed.

HMSC supports variance partitioning, which allowed examination of how much each explanatory variable contributes to the total variance explained for each plant group (Ovaskainen *et al.*, 2017). Further, relationships between plant groups and explanatory (environmental) variables can be examined by extracting relationships that are supported in the majority (90%) of cases from the posterior. For example, a negative relationship indicates that there are fewer individuals of that plant group with that environmental variable. The Markov Chains Monte Carlo (MCMC) chain was run for a total 500 000 iterations and two

chains, with a thinning of 1000 to sample the posterior, after discarding 750 000 iterations as burn-in. The convergence of the MCMC chain was assessed visually by examining the convergence of the results between 10, 100 and 250 thinning. Further, to assess model fit, the Root Mean Square Error (RMSE) and Mean Absolute Error (MAE) were calculated between the observed values and the predicted (posterior distribution) values. MAE measures the average error magnitude, while RMSE incorporates the MAE and the variability within the error distribution, as both are related directly to the model inputs, they increase with the number of individuals in the model (Willmott and Matsuura, 2005).

Results:

Floristics: A total of 8,285 individuals germinated in our study, 5,456 of which were rush species, primarily comprising *Juncus* spp. There were 19 non-grass germinants that we could not grow to identification. Of the 145 grass germinants, only 68 grew to a stage where identification was possible; all other grass and unidentified germinants were removed from the model. Only one individual germinated of *Phyla canescens*, an invasive exotic species of concern in the area. None of the characteristic woody, shrub or clonal species (e.g. river red gum, lignum, black box, river cooba and *Typha* spp.) associated with the floodplain wetlands occurred.

Overall, there was an increasing number of germinants with decreasing levels of land-use (i.e. more in cleared fields, fewer in cultivated fields), and, in the cultivated fields, an increasing number of germinants with fewer cultivation years and time since last land-use event (Fig. 1). The number of exotic germinants was low compared to natives, but they were more abundant in the field Cult. 85-08 (Fig. 2). This heavily cultivated field had the lowest number of native germinants (Fig 2.). In most plant groups, the number of germinants declined with soil depth, although this trend did not always occur for amphibious responders (Fig. 1). Numbers of germinants from native species also decreased with depth, a trend less clear with exotics (Fig. 2). Germinant numbers across the floodplain positions showed that there were more in channel positions than in other geomorphological locations (Fig. 3). The number of individual germinants categorized as amphibious responders and terrestrial dry germinants were variable (i.e. not declining) with depth, particularly in floodplain channels (Fig. 3).

Sample depth alone explained more of the variance in the terrestrial plant groups, while field explained more variance in the amphibious plant groups (with the exception of the

amphibious tolerator emergent group; Fig. 4). RMSE and MAE values show that the models performed reasonably well (Table 2), with higher error rates in groups with the highest number of individuals found on a site, as is expected with these statistics. Variance partitioning showed that most of the variance being explained by the model was attributable to land-use history, with fields alone accounting for a mean 16.3% across the plant groups and the field by sample depth interaction accounting for a mean of 18.9%. The total mean variance explained by fields (land-use history) was 35.2% in the model, demonstrating this variable generally had the highest explanatory power. Sample depth alone accounted for the next largest amount of variance explained (mean of 28.6%), followed by the explanatory variables related to floodplain position accounting (mean of 12.6% for the interaction with depth and 11.8% alone, totalling 24.4%; Fig. 4).

Although fields and field x sample depth interaction had high explanatory power when grouped, individually there were only a few relationships that had at least 90 % support in the posterior (Fig. 5). Surprisingly, a number of plant groups had strong positive relationships with the Clear. 2003 field in comparison to the Clear. 2000 field. Numbers of individual germinants within all plant groups had a weak negative relationship with sample depth (Fig. 5). Furthermore, all native groups, except for amphibious tolerators, were more likely to occur in floodplain channels (Fig. 5). There were numerous weak relationships between the number of individual germinants in both field x sample depth and floodplain position x sample depth interactions. These were all weakly negative, except for the depth x Cult. 2003 field for amphibious responder floating natives and the only supported depth x channel interaction, which were weakly positive. These show that, when compared with the intercept, the posterior showed slightly more or slightly fewer germinants with increasing depth.

Discussion:

Land-use history negatively affected the soil propagule banks down the sampled soil depth profile, with fewer individual germinants belonging to wetland (amphibious) plant groups and increasing number of exotic individuals found in fields that were cultivated more recently or for longer periods. The strong effect of land-use is consistent with both our first hypothesis - that more intensive land-use results in a larger negative effect - and with previous propagule bank studies that have examined only the top 5 cm of soils (Middleton, 2003; Dawson, *et al.*, 2017a). Floodplain positions that were more likely to be inundated had a positive effect on

289 the number of germinants in the soil propagule bank, supporting our second hypothesis - that
290 channel sites would have higher numbers of individuals in the upper layers. We found similar
291 numbers at corresponding depths as the floodplain sites examined by O'Donnell, Fryirs and
292 Leishman (2014), but compared with other wetland types worldwide, there were fewer
293 propagules at corresponding depths (van der Valk and Davis, 1979). However, we found
294 more propagules at similar depths than other habitat types, such as forests (Nicholson and
295 Keddy, 1983; McGraw, 1987; Godefroid, Phartyal and Koedam, 2006). Despite past
296 disturbances in the Macquarie Marshes landscape, amphibious responders and terrestrial dry
297 species did not decrease with depth as expected. This suggests that they form persistent soil
298 propagule banks, providing a temporal storage mechanism effect (Chesson, 2000), which
299 may confer some resilience to disturbances such as drought and low levels of land-use.

300 This is the first study, to our knowledge, that examines the relationships of land-use with the
301 propagule bank depth profile in wetlands, although effects of forestry on soil propagule banks
302 with depth has been investigated in forests (Olano *et al*. 2002). In our study, land-use history
303 and its interaction with depth had the highest level of explanatory power for amphibious plant
304 groups (except amphibious tolerator emergents) and exotic terrestrial dry germinants (Fig. 4).
305 For germinants from other terrestrial groups, explanatory power was more evenly split or
306 dominated by depth (Fig. 4), indicating that land-use history more strongly affected wetland
307 species, even more than soil depth alone. The highest number of exotics, usually undesirable
308 for wetland restoration, were in the field with the longest history of cultivation (Fig. 2).
309 Further, this intensely cultivated field exhibited negative relationships with germinants of
310 amphibious responder native species (Fig. 5) and had less rushes and amphibious responders
311 throughout the soil depth profile (Fig. 1). Clearly, and consistent with our expectations,
312 cultivation had a negative effect on the abundance of native species in soil propagule banks,
313 particularly for amphibious groups, which continued down the soil depth profile.

314 While there is little knowledge of how the propagule bank depth profile changes with land-
315 use, there is a greater understanding of how land-uses discussed here affect propagule banks
316 in the top 5 cm. The findings of this study are consistent with a previous study in the same
317 wetland (Dawson *et al*. 2017a) and another study on the effect of cultivation in floodplain
318 wetlands (Casanova, 2012). All three studies found fewer amphibious species or numbers in
319 cultivated areas, but there were also indications that recovery may be possible, depending on
320 future flooding. It is vital that Australian restoring floodplain wetlands continued to be
321 monitored to evaluate and understand restoration successes and failures (Roberts *et al.*,

2017). While we focused on clearing and cultivation land-use here, other forms of disturbance (e.g. grazing; Nicol *et al.*, 2007) can negatively affect propagule banks as well. Establishing how much different land-uses contribute to propagule bank degradation is important in understanding current restoration attempts and planning future management.

Increased inundation may offset some impacts of land-use history, as floodplain positions prone to flooding were more likely to have higher numbers of germinants from wetland plant groups. Areas with increased flows can support increased deposition events that enable many seeds to accumulate down the soil depth profile (O'Donnell, Fryirs and Leishman, 2014), particularly in cracking vertosol soils. The channel position of the floodplain had higher numbers of propagules from all native plant groups – a trend that persisted down the sampled soil depth profile (i.e. only one very weak channel x sample depth interaction was supported; Fig. 5). Additionally, the Clear. 2003 field had greater numbers of propagules in several native and wetland plant groups, when compared with the intercept, the Clear. 2000 field (Fig. 5). This may seem contrary to expectation as the latter field was cleared a longer time ago (had more recovery time) and was only bulldozed, whereas the Clear. 2003 field was both bulldozed and ripped. However, the Clear. 2003 field has a higher background rate of flooding compared to all the other fields; averaging 18.2 times, compared to averages of 8.8 (Clear. 2000), 9.8 (Cult. 2003), 8.4 (Cult. 06) and 7.1 (Cult. 85-08), using the 32 flooding events that occurred in the 25 years prior to sampling, prior to and during the disturbance (i.e. 1988 to 2012; Dawson, *et al*. 2017b). The difference between the Clear. 2003 field and the other fields was significant, however the differences in the rest of the flood data were not significant, even though the Cult. 85-08 field had slightly fewer floods (Fig. S2). Despite these differences all fields were flooded in events that occurred between 2009-2012: i.e. after the levees were breached and prior to soil sampling (Dawson, *et al.*, 2017a). This increased background flooding in the Clear. 2003 field may account for the higher numbers of amphibious floating individuals observed there (Fig. 1).

Although the propagule banks investigated in this study had more propagules at deeper depths than have been observed in forest and lake soil profiles (Nicholson and Keddy, 1983; Godefroid, Phartyal and Koedam, 2006), there were not nearly as many propagules with depth as have been recorded in prairie marshes (tens of thousands individuals per m^2 at 35 cm depth – if we scale our data using our sampled area to 1 m^2 we have ~5000 individuals at 30 cm) or sphagnum bogs (more than 60 individuals of one species at 29 cm alone - with a core diameter of 9.5 cm; McGraw 1987). Further, the numbers of germinants found here are either

similar to (O'Donnell, Fryirs and Leishman, 2014) or slightly more than (Nielsen *et al.*, 2018) germinant numbers in other Australian floodplain wetlands. Propagule banks in semi-arid Australian floodplain wetlands may therefore effectively be positioned between forests and the more environmentally similar prairie marshes in terms of germinant frequency, possibly due to the strong heterogeneity in these environments, including potentially long periods between floods (Kingsford and Thomas, 1995; Kingsford, 2000). Strangely, van der Valk & Davis (1979) found high abundances of *Typha glauca*, even as deep as 35 cm, whereas we did not have any *Typha* species germinating in either this or the previous study from this wetland (Dawson, *et al.*, 2017a), although this may be due to relatively low abundances of *Typha* in the aboveground vegetation (Dawson, *et al.*, 2017c).

Changes in propagule numbers with soil depth highlights how transient (or short-lived) the soil propagule bank is for different plant groups, which can help understanding of plant strategies. Propagule banks in which the numbers do not steadily or dramatically decrease over the depth profile indicate long-lived propagules that can reside in the soil until favourable germination conditions occur (McGraw, 1987; Olano *et al.*, 2002). This strategy of using propagules in the soil to overcome non-favourable periods for the plant is one mechanism of achieving a temporal storage effect, enabling species coexistence and resilience (Chesson, 2000). In this study, we did not observe strong (or any) declines in propagule numbers with depth for either amphibious responders (both floating and plastic in the less disturbed sites) or the terrestrial dry group, showing they likely form persistent propagule banks (Brock, 2011). Species in these plant groups are generally short-lived (i.e. < one year) and the conditions suitable for either group (i.e. inundation or dryness) occur at intermittent, discrete intervals. Therefore, it is likely that species in these groups form substantial persistent soil banks as part of a temporal storage effect, enabling persistence in location over the long-term. Although the rush plant groups did decline in a way associated with transient soil propagule banks, the sheer number of germinants indicated that these species also rely on the temporal storage effect, through a large propagule bank. Others have found similarly large numbers of rushes (particularly *Juncus* spp.) with increasing soil depths in wetlands (van der Valk and Davis, 1979; McGraw, 1987), and even forest habitats (Olano *et al.*, 2002), which was also attributed to a species strategy of awaiting perturbations to germinate.

While this study is the first examination of how land-use disturbance affects soil propagule bank depth profiles in Australian wetlands, there were three shortcomings. First, although we

chose germination conditions that supported the largest number of germinants in a previous study (Dawson, *et al.*, 2017a), it is unlikely that these conditions suited all species, meaning that we may have failed to detect some species present in the soil propagule bank (e.g. see Nielsen *et al.*, 2018). Second, the deposition rates of both propagules and soil probably change across the floodplain in relation to topographic position, in turn affecting rates of change in the propagule bank over the soil depth profile. Lastly, the soils of this floodplain often form large, deep cracks when completely dried (cracking clays; personal observation). Although we ensured samples were not near any current cracks, seeds may have fallen down previous cracks in the past, altering the depth profile that would occur from gradual accumulation of soil layers. This would be consistent with what has been found in seasonally drying salt-marshes (Espinar, Thompson and Garcia, 2005; Espinar and Clemente, 2007) and may account for some of the higher numbers seen at greater depth for amphibious responder species.

Examining how past degradation has changed the propagule depth profile provides insights into the nature of past land-use and disturbances. Past land-use was the most important factor influencing the depth profile of propagule banks and this was most apparent amongst native and amphibious plant groups. However, channel and riparian floodplain positions or increased background rates of inundation were associated with greater propagule abundances of native and amphibious species, both desirable for restoration. Further, amphibious responder species appeared to be persistent in the propagule bank, which is encouraging for projects aiming to use the soil propagule bank to restore degraded but uncultivated areas. As well as amphibious responders, terrestrial dry groups also formed persistent propagule banks, and each of these groups generally consists of species with shorter life cycles and that have longer periods between germination events, indicating that these species rely on the propagule banks as a temporal storage mechanism.

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548

549 **Tables and Figures:**

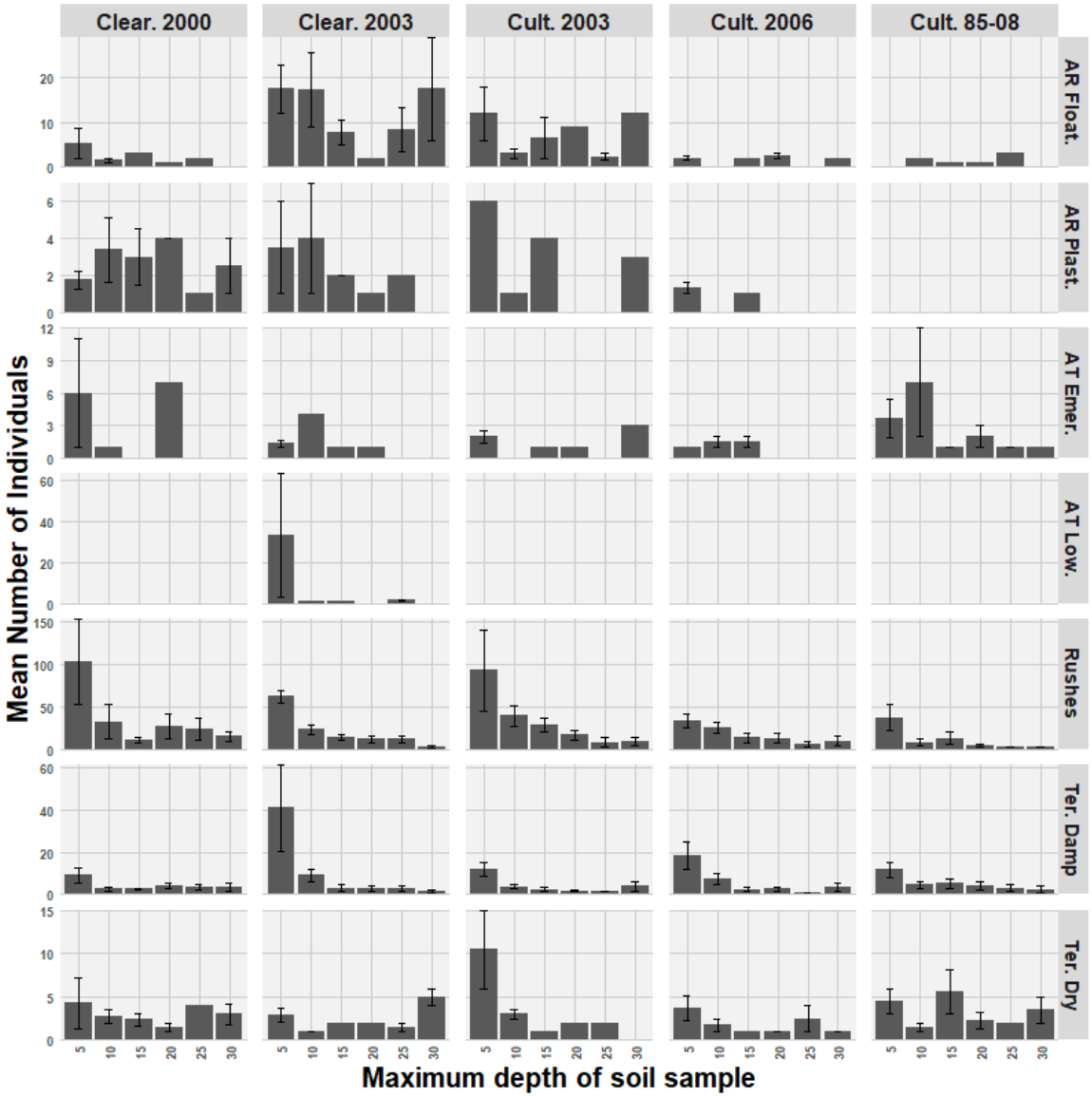
550 **Table 1:** Description of plant groups, based on Brock & Casanova (1997), with functional
551 groups divided into native and exotic where applicable and the rushes species complex. This
552 group fits within the amphibious tolerator emergent family, but as this species complex had
553 very high numbers germinating, we chose to separate it for the purposes of this study.

Full plant group name	Shortened name for figures	Description
Amphibious responder, floating (native species)	AR Float.	Species with floating leaves that can grow in damp to flooded conditions, germinate when flooded and has floating leaves in response to inundation
Amphibious responder, morphologically plastic (native species)	AR Plast.	Species that are morphologically plastic, which can grow in damp to flooded conditions, germinate when flooded and is morphologically plastic in response to inundation
Amphibious tolerator, emergent (native species)	AT Emer.	Emergent species that germinate in damp to flooded conditions, tolerate variation in inundation with basal parts submerged and reproduce above water
Amphibious tolerator, low-growing (native species)	AT. Low.	Low-growing species that germinate in damp to flooded conditions, tolerate variation in inundation and can be completely submerged
Rush species, (*Juncus* spp.; native species)	Rushes	Germinants that were rush species, predominately composed of *Juncus* spp.
Terrestrial damp (native species)	Ter. Damp	Native species which complete some or all of their lifecycle on saturated soil
Terrestrial damp (exotic species)	Ter. Damp E.	Exotic species which complete some or all of their lifecycle on saturated soil
Terrestrial dry (native species)	Ter. Dry	Native species that complete their life cycle where there is no surface water
Terrestrial dry (exotic species)	Ter. Dry E.	Exotic species that complete their life cycle where there is no surface water

554

Table 2: Values for the Root Mean Square Error (RMSE) and Mean Absolute Error (MAE) statistics used for model evaluation for each plant group. These values can be used to assess how well our models are characterising each plant group. Values are calculated from comparing the numbers predicted by the model with the raw data. MAE shows the average error magnitude; i.e. on average how far are predicted values from actual values. RMSE incorporates both MAE and the variability within the error distribution. Both values will increase with increasing numbers of individuals in the plant group (e.g. we had far more rush species in the model than any other group). Full plant group names can be found in Table 1.

Plant Group	**RMSE**	**MAE**
AR Float.	**9.67**	**4.11**
AR Plast.	**1.03**	**0.42**
AT Emer.	**1.19**	**0.52**
AT. Low.	**5.64**	**0.43**
Rushes	**42.66**	**26.92**
Ter. Damp	**14.28**	**4.52**
Ter. Damp E.	**2.12**	**0.61**
Ter. Dry	**1.68**	**1.02**
Ter. Dry E.	**1.5**	**0.49**



565

566 *Figure 1: Mean number of germinants (with standard error) of each plant group within each*
567 *field (per 98.15 cm^3); note: Y axis changes depending on the maximum number found in each*
568 *group and groups that are divided into natives and exotics for the analysis are combined here*
569 *(see Fig. 2 for native versus exotic distribution). Fields are arranged by the level of past*
570 *land-use: cleared with bulldozer in 2000 (Clear. 2000), cleared with bulldozer and ploughed*
571 *in 2003 (Clear. 2003), cultivated in 2003 (Cult. 2003), cultivated in 2006 (Cult. 2006) and*
572 *cultivated from 1985-2008 (Cult. 85-08). Plant groups (also found in Table 1) from top to*
573 *bottom are: amphibious responder, floating (AR Float.), amphibious responder,*
574 *morphologically plastic (AR Plast.), amphibious tolerator, emergent (AT Emer.), amphibious*
575 *tolerator, low growing (AT Low.), rush species, dominated by Juncus spp. (Rushes),*
576 *terrestrial damp (Ter. Damp) and terrestrial dry (Ter. Dry).*

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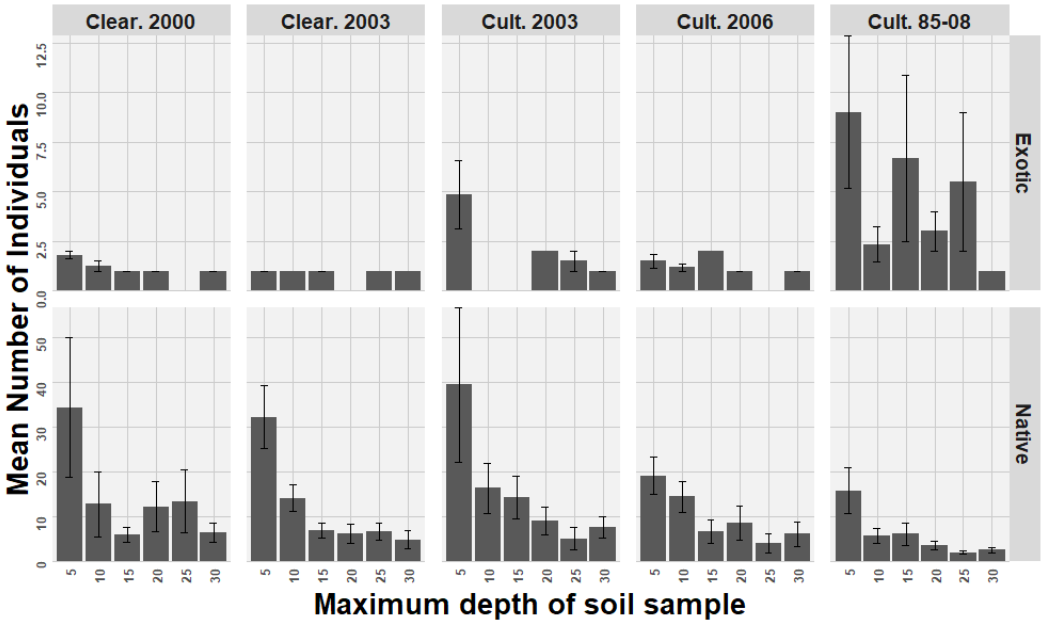
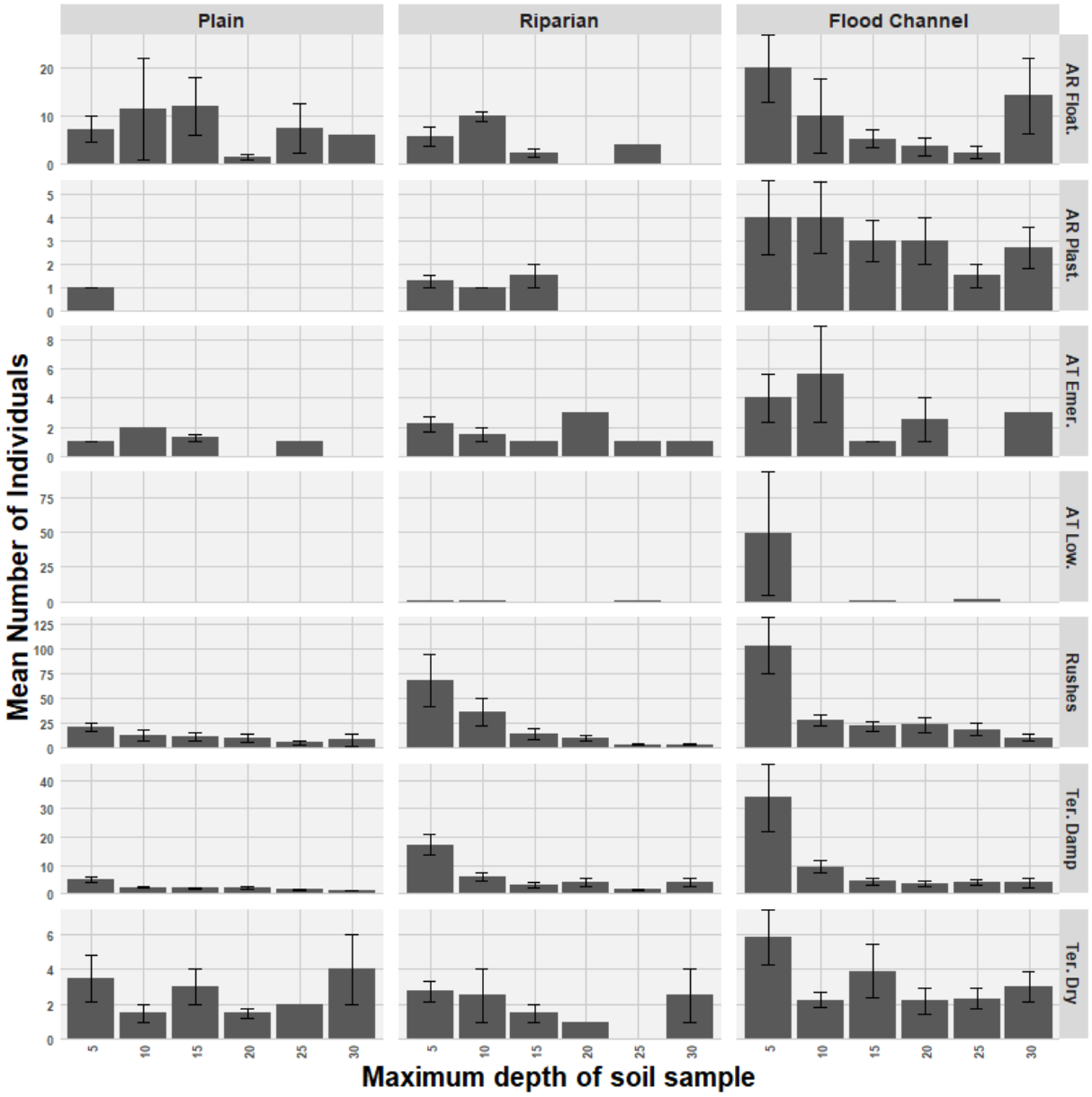


578

579 *Figure 2. Mean number of germinants (with standard error) of natives and exotics within*

580 *each field (per 98.15 cm^3). Fields are arranged by the level of past land-use (see Fig. 1).*

581



582

583 *Figure 3: Mean number of germinants (with standard error) of each plant group within each*
584 *floodplain position (native and exotics that are separated for the analysis are combined here;*
585 *per 98.15 cm^3). Floodplain position is arranged from least to most frequently inundated:*
586 *plain positions 50-100 m from nearest micro-channel (Plain), sites located immediately*
587 *adjacent to floodplain micro-channels (Riparian) and within the floodplain micro-channels*
588 *(Channel). For full plant group names see Fig. 1 caption.*

589

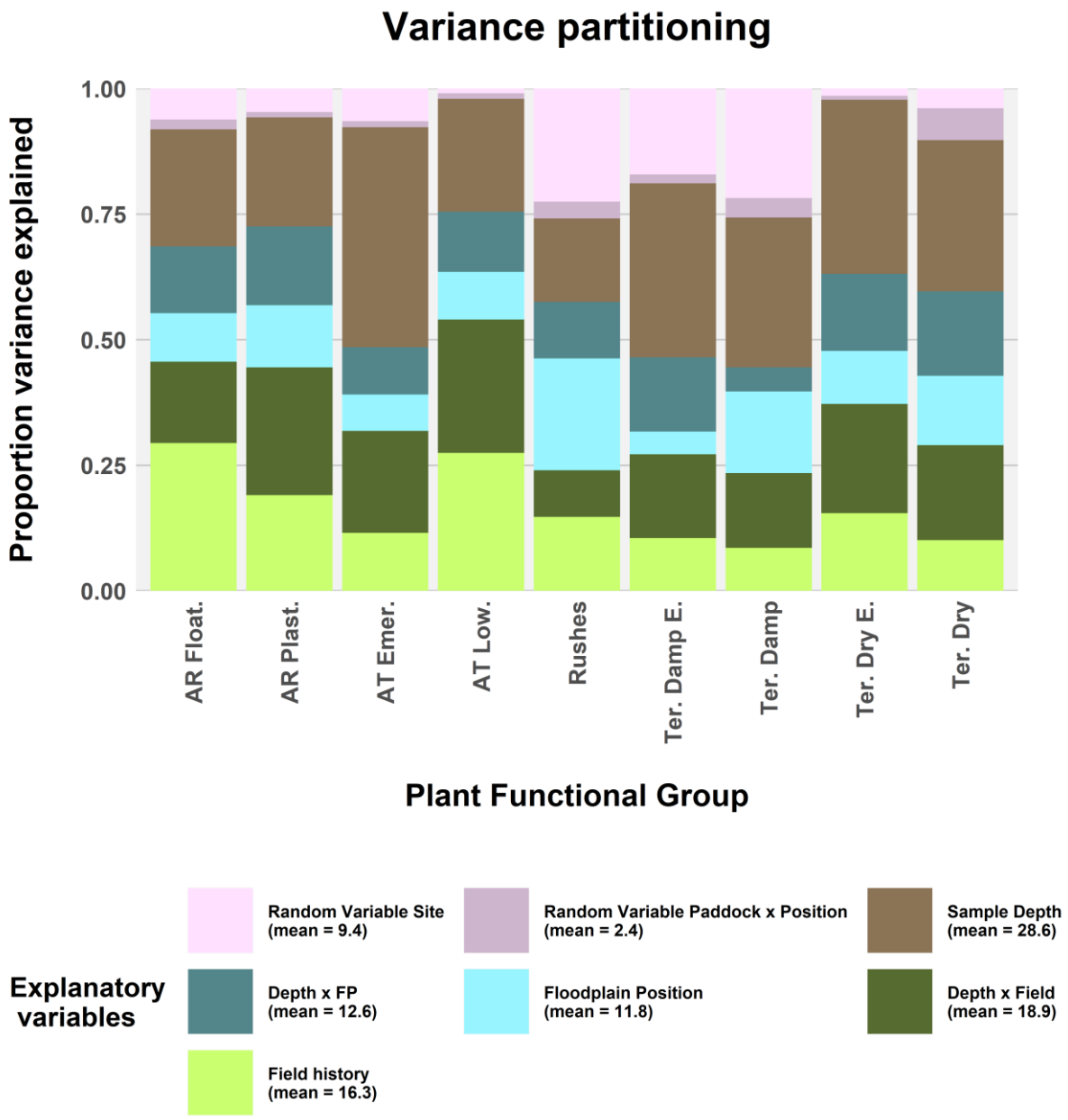
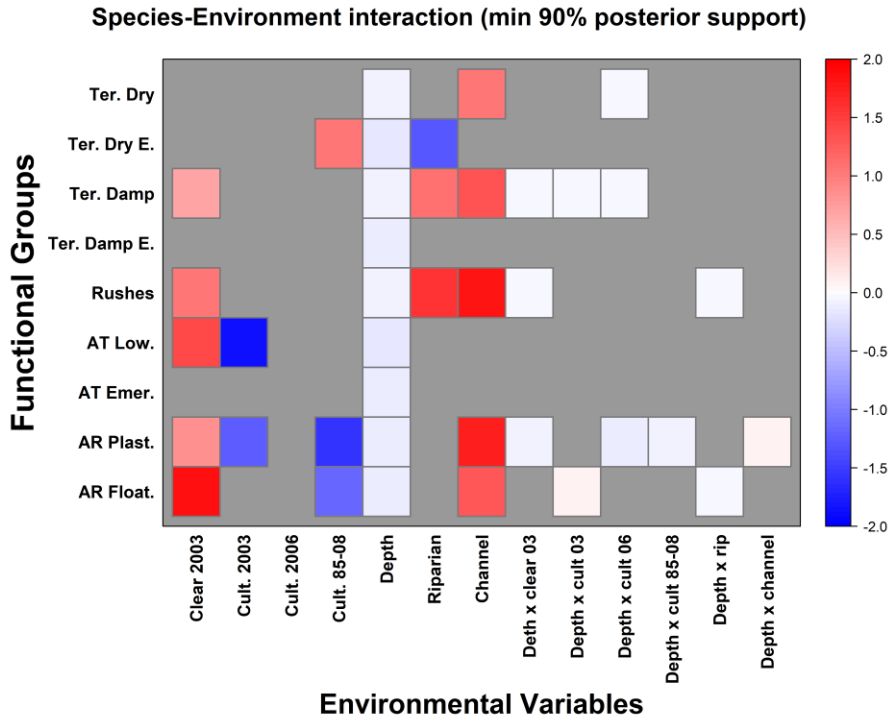


Figure 4: Variance partitioning plot showing the proportion of each set of explanatory variables contributing to the total variance explained. Note: the total variance explained would be different for each plant group; this figure demonstrates what each part of the model is contributing to the variance that the full model can explain (not equivalent to R^2, for model evaluation see Table 2). Each set of explanatory variables in the key represents several single explanatory variables (e.g. Fields represent all variance explained by the four fields against the intercept), except for Sample Depth, which is a continuous variable. For full plant group names see Table 1.



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602 *Figure 5: Relationships between explanatory variables and plant groups that had at least*
603 *90% support in the posterior distribution in relation to number of germinants. The intercept*
604 *for each group of explanatory variables is Clear. 2000 for the Fields and Plain for the*
605 *Floodplain Position, meaning the displayed relationships are relative to each of these (i.e.*
606 *Clear. 2003 had more AR Float. than Clear. 2000 in 90% of posterior sample). Names of*
607 *plant groups follow Fig. 4 with the fields and floodplain positions following Figs 1 and 3.*
608 *Red indicates increasing numbers of germinants (values logged) with that variable (i.e. the*
609 *model predicts more rush germinants in channel sites then plain sites or more amphibious*
610 *responder floater germinants in Clear. 2003 sites than Clear. 2000 sites). The blue indicates*
611 *the inverse relationship (i.e. fewer predicted amphibious responder plastic germinants in*
612 *Cult 85-08 sites than Clear. 2000 sites or fewer predicted terrestrial dry exotic germinants in*
613 *riparian sites compared with plain sites).*

614